INHERITANCE OF OIL CHARACTERS IN EUCALYPTUS.

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(Five Text-figures.)

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Synopsis.

Examination of segregates from E cinerea $\times E$. Macarthuri and E. pauciflora $\times E$. Robertsoni or E. dives, together with F1 hybrids between E. Maideni $\times E$. rubida, shows that recombination between oil yield and components on the one hand and morphological characters on the other occurs. Yield is sometimes determined in a far-reaching way in accordance with that of one parent. The variance of physical and chemical constants of oils derived from segregating hybrids is much greater than that of those for the parents. Oil constituents may be found in much greater quantity in some segregates than in either parent.

It has been evident that oil characters of Eucalypts, especially yield and the nature of their various constituents, are determined to a large extent by heredity. The review of the genus by Baker and Smith (1920) and their attempt to develop its taxonomy by the consideration of oil composition shows the high degree of oil specificity which species have sometimes been found to possess. On the other hand, something is also known about the variation within species largely as a result of the recognition of "physiological forms" by Penfold and Morrison (1927) in *E. dives*. Such forms are more or less similar morphologically, differing mainly in the chemical nature of their oils. These have been found since also in many other species of Eucalypts as well as in other genera of the Myrtaceae.

A study by Willis (1951) of families planted in one locality, made up of several progenies from different oil varieties of E. dives from different localities, showed that within this species the characters of the parents were largely repeated in the progeny too. Bryant (1950) has summarized unpublished work carried out with Smith-White indicating that wide variations in oil yield occur within a number of commercially important species. Major constituents of the oils were also shown to vary within the species and also even within a single tree but there has been little study of the variation in minor components.

The biological significance of essential oils in plants has not yet been clearly established, although different theories have been advocated. Two main ideas may The first, held by James (1953) and others, suggests that in plants be mentioned. generally, constituents such as alkaloids or essential oils are produced as a by-product of metabolism and have no adaptive significance. The second, demonstrated in some plants by Dethier (1941) and held by Barber (1955) for Eucalypts (and oil or alkaloid bearing plants generally), is that the varying characters of the oils indicate part of a system which is of distinct adaptive value by determining the palatability or resistance to insect pests. It has not yet been established for Eucalyptus that palatability to insects is influenced by the chemical nature of the essential oil, but if this is so one could imagine through time a sequence of changes both in oil composition and insect variation, leading to a series of alternating changes in closely adaptive responses in both plant and insect. Dethier (1941), using pure compounds found in the oils of some species of the Rutaceae and Umbelliferae, was able to induce Papilio larvae to eat filter paper treated with them and so indicate positive attraction by them for these insects. In *Eucalyptus* strong preferences by leaf-eating insects are

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already known, and in one or two combinations there is evidence that this is an inherited character (Pryor, 1953). It is possible that the major oil constituents in *Eucalyptus*, while of great consequence in a similar system in some earlier evolutionary period, may now be of little importance, and the real significance as far as insect attack is concerned may rest with quantitatively minor constituents.

There is considerable interest, therefore, both from the point of view of evolutionary genetics and in understanding physiological forms, in gaining knowledge of the mode of inheritance of oils in *Eucalyptus*. The study might also provide basic information which could lead to very important results in applied work, such as in the control of insects feeding on *Eucalyptus* on the one hand and in the *Eucalyptus* oil industry on the other. Investigation can proceed some distance by raising progeny from open pollinated natural hybrids which give access to segregating groups of individuals containing recombinants derived from pairs of parent species. This will permit some deductions concerning the inheritance of oil characters.

Method.

Combinations of parent species were selected which showed some strongly contrasting characters both in oils and morphology. Open pollinated progeny raised from naturally occurring hybrids have been examined at about the age of six years. Progeny of the parents of the same age, raised at the same time, have been compared. The offspring of parents (supposedly the "pure" species) are not necessarily of precisely the same stock which led to the production of the hybrids, and there is a potential source of error here which imposes some limitations on the interpretation of the data, and may account for some minor anomalies which have been found.

The crude oil samples were obtained by steam distilling 10 lb. of green leaves and small twigs collected in the same way and in the same position from each of the trees. Approximate weighing to a little more than 10 lb. with a spring balance was carried out in the field, and a more precise weighing to reduce the sample to 10 lb. $\pm \frac{1}{4}$ oz., was made in the laboratory. The leaves were steam distilled to obtain the first oil sample. The physical and chemical analyses were carried out by one of us (Bryant). Two sets of data were compiled. Firstly, the constants usually calculated for essential oils were established, particularly specific gravity, refractive index, optical rotation and saponification number. Secondly, by a method of circular chromatography (Bryant, 1955) using glass coated with magnesol, an assessment of most of the oil components was made. The oils were developed with n.hexane containing 15 parts by volume of ethyl acetate and then sprayed with concentrated H_2SO_4 or examined under ultra-violet light. Most of the oil constituents reacted with the H₂SO₄ to give characteristic colours. Cymene and the pinenes did not react satisfactorily and, although they are known to occur to some extent in these oils, their proportion was not assessed. To assess recombination between oil features and other characters, measurements of selected leaf features were made as well. In some, the leaf shape as indicated by the length-breadth measurement was used, and in others the angle which the primary veins made with the midrib. Transformation of the length-breadth figures to a logarithmic scale results in reducing the variance of the data for the parents in each case to more nearly the same level, and makes the relationship clearer between the various groups and intermediates.

A small amount of material was also available from F1 hybrids produced by manipulation, and this, though limited in extent, gives some additional indications of the inheritance pattern.

E. cinerea \times E. Macarthuri.

The hybrid *E. cinerea* \times *E. Macarthuri* is found naturally from time to time where these two species meet in the field. Two segregating progenies were raised from two separate hybrid trees of this combination found at Paddy's River on the Hume Highway near Marulan, N.S.W., from which open pollinated seed was collected. The parent trees differ widely in morphological and oil characters. Table 1 shows the principal physical differences between the two species. Table 2 and Figures 1*a* and 1*b* show the range of variation of oil and morphological characters within the parent species and in the segregates. These latter show marked segregation and recombination of both characters, and contain individuals which closely resemble either parent together with a series of intermediates between them.

—	E. cinerea.	E. Macarthuri.		
uvenile leaves	 Orbicular.	Lanceolate.		
	Sessile.	Sessile.		
	Glaucous.	Green.		
Mature leaves	 Sessile.	Petiolate.		
	Opposite.	Alternate.		
	Glaucous.	Green.		
Dil yield	 High (about 1.75% vol./wt.).	Low (about 0.25%).		
Iain constituents	 High cineole (about 40%).	Cineole nil.		
	Geranyl acetate (nil).	Geranyl acetate (about 50%).		

In the hybrid progeny 50/755a there are more segregates approaching *E. cincrea* than *E. Macarthuri*. In 50/755 they are approximately evenly distributed between the parental limits. It will be noticed that the quantity of oil produced in both hybrid progenies is within the range of the low-yielding parent (*E. Macarthuri*), and there is not a single exception to this (Fig. 1a). This suggests, therefore, that

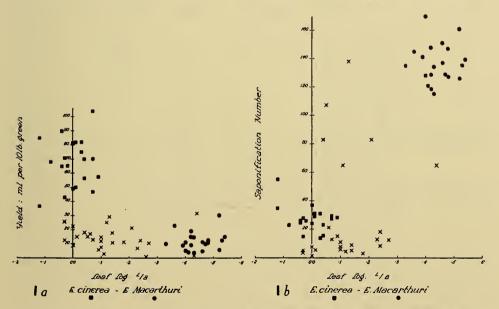


Fig. 1a.—Yield of oil in ml. per 10 lb. of green leaf against juvenile leaf shape is shown. The "x's" indicate hybrids. It will be seen that the leaf shape in the hybrid progeny ranges between either parent, but that the oil yield is entirely within the range of the E. Macarthuri parent.

Fig. 1b.—Saponification number in relation to leaf shape shows in this particular progeny a tendency for the E. *cinerea* characteristic of low saponification number to persist in the hybrid progeny indicated by the "x's", but there are some recombinants which have E. *cinerea* leaf shape but saponification number equal to that of E. *Macarthuri* and one which is the reverse.

the factors determining quantity of yield in the *E. Macarthuri* parent are dominant in this combination, and they determine low yield. On the other hand, it will be seen that the amount of geranyl acetate in the oil assessed by saponification number, when compared in relation to the morphological character of leaf shape, shows distinct evidence of recombination. Hybrids 23 and 34, while having a leaf shape which

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approaches that of E. cinerea, have a saponification number which is closely comparable with that of E. Macarthuri, whereas, on the other hand, No. 16 has a leaf shape which is near the centre of the range of E. Macarthuri, but has a much lower saponification number. In the data as a whole there is low correlation between leaf shape and saponification number, which suggests rather free recombination between these two characters (see Fig. 1b). Both hybrid progenies are somewhat limited, and a considerably larger population would be desirable to assess more accurately the pattern of recombination, and to determine whether there is any tendency for characters to recur in association in any degree, perhaps suggesting linkage.

In Table 2 the presence of the various constituents of the oils (excluding terpenes such as the pinenes already mentioned which do not react readily with concentrated H_2SO_4) has been assessed by the chromatographic method mentioned above. It will be observed that cineole and geranyl acetate, which could not be detected in the parent *E. Macarthuri* and *E. cinerea* oils respectively, are both present together in the oils of some of the hybrid individuals. In no case is there a hybrid oil where both these constituents are absent. Geraniol, present in small quantities in all

—	No.	Geranyl Acetate.	Geraniol.	Cineole.	Eudesmol.	Eudes- mene.	Sesqui- terpene.	Fluo- rescent Com- ponent
	52	××××	×		×××	×	×	×××
	53	$\times \times \times \times$	×	-	X X X	×	×	×××
	54	$\times \times \times \times$	×	-	X X X	×	' ×	×
	55	XXXX	×	-	×××	×	×	×××
	56	XXXX	×	-	XXX	×	×	X·X
	58 59	$\begin{array}{c} \times \times \times \times \\ \times \times \times \times \end{array}$		_	××× ×××	× ×	X X	×
	61	× × × × ×	x		××××	×	×	
	63	XXXX	×		XXX	x	×	
E. Macarthuri.	64	XXXX	x	_	××××	×	×	××
	65	XXXX	×		×××	×	×	_
	67	××××	×	-	×××	×	×	×
	68	××××	×	-	×××	×	×	×
	70	$\times \times \times \times$	×	_	X X X	×	×	×
	71	$\times \times \times \times$	×	-	X X X	×	×	× ×
	74	$\times \times \times \times$	×	-	X X X	×	×	-
	77	$\times \times \times \times$	×	-	X X X	×	×	-
	79	$\times \times \times \times$	×	-	X X X	××	×	-
	80	$\times \times \times \times$	×	-	$\times \times \times$	×	×	-
	81	× × × ×	×	-	$\cdot \times \times \times \cdot$	×	×	_
	40	-	×	××××	×	_	-	-
	41		<u>×</u>	$\times \times \times \times$	-	×	X X	×
	42	-	× × ×	$\times \times \times \times$	-	×	××	×
	43	-		$\times \times \times \times$	-	×	××	-
	45	—.	-	$\times \times \times \times$	-	×	X X	-
	46	-	—	$\times \times \times \times$	-	×	X X	××
	47	-	-	XXXX	-	×	××	-
	48 49	1 -	<u>×</u>	$\begin{array}{c} \times \times \times \times \\ \times \times \times \times \end{array}$	-	÷	××	-
E. cinerea.	49		_		- ×	$\hat{\mathbf{x}}$	×××	×
D. cinerea.	85	_	_	××××		$\frac{1}{X}$	× ×	<u> </u>
	88	_	_	XXXX	_	×	××	_
	100	_	_	XXXX	×	×	x	
	102	-	— .	××××	×	×	×	×
	104	-	×	XXXX	<u>×</u> <u>-</u>	×	×	
	111	-	· ×	$\times \times \times \times$		xix x x x x x x x x x x x x x x x x	×	-
	112	-	×	$\times \times \times \times$		×	×.	×
	113	-	-	$\times \times \times \times$	×	×	$\mathbf{x} = \mathbf{x} \mathbf{x}_{0}$	
	114	- ,	-	XXXX		×	××	×××
	?	-	×	XXXX	X	×	X	×

 TABLE 2.

 Oil Constituents (Except Cymene and Pinenes) of cinerea, Macarthuri and Hybrids.

	No.	Geranyl Acetate.	Geraniol.	Cineole.	Eudesmol.	Eudes- mene.	Sesqui- terpene.	Fluo- rescent Com- ponent.
	1	×	_	_	×	×××	×××	×××
	3	1 1	-	×	×	$\times \times \times$	× ×	× × ×
	4	×	_		X	$\times \times \times$	X X	×××
	5	× ×	×	_	××	×х	××	×××
	8	_	×	×		$\times \times \times$	× × ×	×××
	11	-	×	×		$\times \times \times$	×××	×××
	12	_	-	××	×	$\times \times \times$	× × ×	×××
	13	_	×	×××		$\times \times$	× ×	×××
	14	× ×	_	××	× ×	××	X X	
	15	-	×	×××	×	××	× ×	× × ×
	16	× ×	_	_	X X	××	××	× × ×
	17	××	×	×	× ×	$\times \times$	× ×	×××
	18	- 1	×	×	×	$\times \times \times$	× ×	× × ×
Hybrids.	21	-	××	×	×	$\times \times \times$	X ×	×××
	22	_	_	××	×	×	×××	_
	23	×××	××	_	×××	××	-	×××
	24	×	×	XXX	×	××	× × ×	× ×
	25	Not recorded				$\times \times \times$	×××	×××
	26	×	××	X X X	××	$\times \times \times$	× ×	××
	27	×	×	$\times \times \times$	XX	$\times \times \times$	× × ×	××
	29	-		××	×	$\times \times \times$	$\times \times \times$	× ×
	32	_	××	×××	×	$\times \times$	X X X	× ×
	33	×××	××	××	×	×	× ×	×××
	34	××	××		×××	×	×	×× ·
	35	-	××	××	×	×х	×××	××
	36		×	××	××	$\times \times \times$	×××	× × ×
	38	-		$\times \times \times \times$	× ×	×х	××	××

 TABLE 2.—Continued.

 Oil Constituents (Except Cymene and Pinenes) of cinerea, Macarthuri and Hybrids.—Continued.

E. Macarthuri oils, is present but in still smaller quantities in only 25% of the E. cinerea parent oils and in 60% of the hybrids. In 22% of the hybrids it is present in greater quantity than in any of the parent E. Macarthuri oils.

The sesquiterpene alcohol, eudesmol, which is present to the extent of about 15% in all the parent *E. Macarthuri* oils, is largely absent from the *E. cinerea* parents but is present in all the hybrids, sometimes in quantities as large as the *E. Macarthuri* parents. Eudesmene, though present in small amounts in all the oils of the *E. Macarthuri* parents, is present at the most as a trace in the *E. cinerea* parent but present in all the hybrids, over 50% showing considerable amounts.

The unidentified sesquiterpene is present in almost all oils. It is in greater amount in *E. cinerea* than in *E. Macarthuri* and still greater than either in the hybrids. The fluorescent compound is present in about half the oils of both parents, whilst in the hybrids 93% contain larger individual amounts than either of the parents.

With regard to the specific gravity, refractive index and optical rotation of the oils, the parents show relative uniformity within themselves, but the hybrids display wide variation in these properties. In this respect hybrid 29 with its low specific gravity and high laevo-rotation is of interest. This could be due to the presence of substantial quantities of l-pinene but was not further investigated. The means of the physico-chemical constants of the hybrids lie between those of the parents excepting in the case of the refractive index (Fig. 4). This is explained by the larger quantities of sesquiterpene present in the hybrid oils.

It is clear from these data that recombination of oil constituents is a feature of the hybrids of this cross. Gershtein (1951) studied the oils of a number of Eucalypts and their hybrids. The only chemical constituent assessed was cineole which did not vary greatly in parents or hybrids. The physico-chemical constants published by him, however, indicate that the hybrids contain similar constituents to those found in the parents. Mirov (1932) in *Pinus* turpentines has described a *P. ponderosa* \times *P.*

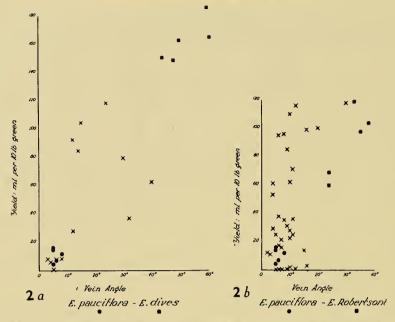


Fig. 2a.—Intermediate position of the hybrids in yield in relation to vein angle is illustrated, although there is a preponderance in the progeny of individuals which are identical with the *E. pauciflora* parent and none actually quite reaches the range of the *E. dives* parent.

Fig. 2b.—E. pauciflora \times E. Robertsoni. Hybrids are indicated by x. Again many of the hybrid individuals are intermediate, but some are identical with either parent. It will be noticed, however, that the recombinants occur in one way only, an individual with a low vein angle sometimes has a high oil yield instead of the normal low yield characteristic of the *E. pauciflora* parent, but the reverse, i.e. a high vein angle and low oil yield, does not appear in the material examined.

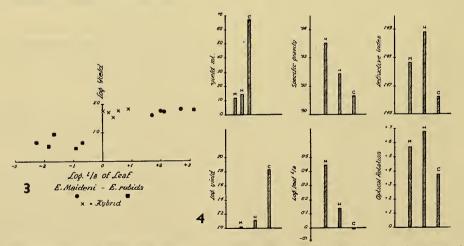


Fig. 3.—The F1 hybrid E. Maideni \times E. rubida is compared with the "pure" parents in oil yield. It is clear that the F1's are entirely in this respect identical with the E. Maideni parent.

Fig. 4.—The means of various physico-chemical characters of the *E. Macarthuri* \times *E. cinerea* oils and the hybrids. Three separate conditions are illustrated and in yield the hybrids are almost identical with the low-yielding parent. In specific gravity and leaf shape the hybrids are approximately intermediate between the parents. In refractive index and optical rotation the characters of the hybrids taken as a group considerably exceed those of either of the parents.

Jeffreyi hybrid containing terpenes inherited from the *ponderosa* parent and heptane from the Jeffreyi parent. Work by Snegirev (1936) on F1 and F2 hybrids of two species of Ocimum shows a similar situation in inheritance of oil constituents in the F1 hybrids. However, F2 hybrids in this case on the basis of specific gravity, refractive index and optical rotation data he considered showed "that the composition of the oil in these hybrids had undergone profound changes".

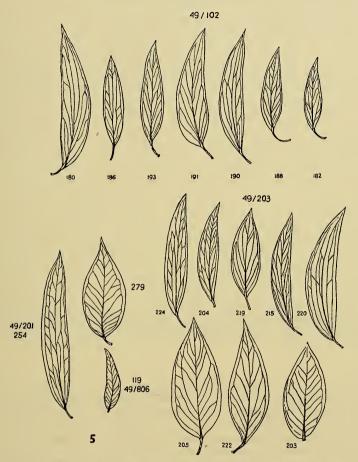


Fig. 5.—Typical examples of the leaf venation of the parents are shown: No. 254, E. pauciflora; No. 279, E. dives; and No. 119, E. Robertsoni. All are intermediate leaves taken from trees of the same age on about the third pair of leaves on a shoot about four feet from the ground. No. 49/102 indicates the range of venation pattern in the hybrid progeny, E. pauciflora \times E. Robertsoni, and No. 49/203 in E. pauciflora \times E. dives.

Although no evidence of new compounds (i.e. compounds not present in the parents) was found in the oils of the hybrids, *E. cinerea* \times *E. Macarthuri*, the considerable increase in the content of eudesmene, unidentified sesquiterpene and fluorescent component is of interest, since they exceed substantially the amounts of these materials present in either parent.

E. pauciflora \times E. Robertsoni and E. pauciflora \times E. dives.

No analysis has been made of the oil components in these combinations, but they afford a good opportunity to examine the inheritance of oil yield in relation to morphological characters. Figure 2 shows the leaf character which has been compared with oil yield, and the various yields obtained with the assessment of the vein angle of the different individuals (Fig. 5). In the progenies 49/104 and 49/102 there is very distinct segregation, and a wide range of variation between the two parents, and the same is true of 49/203 in relation to *E. dives*. Unlike the previous hybrid combination the character, oil yield, segregates and recombines freely. In each hybrid progeny there are some individuals of the same order as either parent with a full range of intermediates. There is also distinct recombination between the character of leaf vein angle and oil yield, as illustrated by Figure 2.

Sampl	e.	Cincole.	Eudesmol.	Fluorescent Component.	Outer Sesqui- terpene Eudesmene.	Inner Sesqui- terpene.	Component Just Behind Eudesmol.	Component Just in Front of Inner Sesqui- terpene.
M×M Self	267	$\times \times \times \times$	×	· · · ·	×	×	×	×
$\mathbf{M} \times \mathbf{M}$	301	$\times \times \times \times$	×××	_	× × × × ×	×	×	×
$\mathbf{M} \times \mathbf{M}$	302	××××	× × •	-	×	×	×	×
$\mathbf{M} \times \mathbf{M}$	303	$\times \times \times \times$	× ×	-	<u>×</u>	×	×	×
$\mathbf{M} \times \mathbf{M}$	304	$\times \times \times \times$	××	-	×	× .	×	×
M×R (F1) 297	$\times \times \times \times$	×	_	×	×	×	×
M×R .	298	×××× `	XIX :-	_	×	××	×	×
$\mathbf{M} \times \mathbf{R}$	299	$\times \times \times \times$	×	. –	×	×	×	×
$\mathbf{M} \times \mathbf{R}$	300	$\times \times \times \times$	XXX	-	×	××	×	×
$\mathbf{M}\times\mathbf{R}$	264	×××	×		× × × ×	×	×	×
$\mathbf{R} imes \mathbf{R}$	309	××	×××	××	××		× x	××
$\mathbf{R} \times \mathbf{R}$	310	$\times \times \times$	××	××	×	$\times \times \times \times$	× ×	×
$\mathbf{R} \times \mathbf{R}$	313	$\times \times \times$	× × Y	××	×	$\times \times \times \times$	°, ××	×
$\mathbf{R} \times \mathbf{R}$	311	$\times \times \times$	' × × ¹⁰	× ×	×× .	××××	× x	×
$\mathbf{R} \times \mathbf{R}$	312	$\times \times \times$	×× "	××	× .	××× ×	×	×
		· · · · ·	1					

TABLE 3.	
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Note.—All oils examined gave fluorescence in P. cymene zone of similar intensity. This component would be expected to be present. Pinene is probably also present in all species, but its Rf being similar to that of the outer sesquiterpene (eudesmene) results in confusion with this component on reacting with conc. H_2SO_4 .

M = Maideni. R = rubida.

F1 Hybrids.

The hybrid studied principally in relation to the parents is E. Maideni $\times E$. rubida. The oil constituents in the parents are rather similar. Quantitatively, however, E. rubida is a very low yielding species giving about 0.1% oil, whereas E. Maideni is reasonably high, giving about 1.4% oil. The various components of the oil have been assessed chromatographically, as shown in Table 3. The most striking differences exist in the "fluorescent component", the sesquiterpene and the component "near eudesmol". In the case of the fluorescent component and the component near eudesmol, the F1 hybrid is like the E. Maideni parent. In the case of the sesquiterpene, it appears to be intermediate, although the data are not fully consistent. There are no differences between the cineol and eudesmol contents in the parents and none in the hybrid. A similar examination has been made of E. cinerea \times E. Blakelyi F1 hybrids, but the differences between the parents are not sufficiently striking to derive any conclusions from the limited material available. In the E. Maideni \times E. rubida the same kind of inheritance pattern is displayed with regard to yield as in the E. cinerea \times E. Macarthuri combination, but on this occasion it is reversed, and in the F1 the yield is identical with that of the high yielding parent (Fig. 3). Gershtein's (1951) figures for the F1 E. Maideni \times E. viminalis show a similar position. At the same time there is a tendency for the constitution of the E. Maideni parent to be followed in the oil combinations; this suggests that the determinants of the yield and certain of the constituents derived from E. Maideni in this F1 hybrid are displaying dominance, perhaps like the determinant of the red pigment of the Rutgers tomato (Tomes et al., 1952).

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Discussion.

While the material available does not permit an exhaustive analysis of the pattern of inheritance, it indicates some interesting aspects. It seems that the yield may be determined by one parent in a very far-reaching way, as is shown by the E. cinerea \times E. Macarthuri segregating populations and also in the E. Maideni \times E. rubida F1 hybrid. The same may be true of some of the different components, as is indicated in the fluorescent component in the E. Maideni \times E. rubida F1. On the other hand, in some combinations, as the E. pauciflora $\times E$. Robertsoni and E. pauciflora $\times E$. dives, there is very distinct segregation and recombination of yield, as there is also for geranyl acetate in the E. Macarthuri $\times E$. cinerea combination. In the E. cinerea \times E. Macarthuri and the E. pauciflora \times E. Robertsoni and E. pauciflora \times E. dives there is evidence of recombination of various characters. In the first place it is between oil constituent and leaf shape, and in the second place between yield and angle of leaf vein. The morphological characters within these combinations have been selected for ease of measurement. There are several characters less easy to measure, as for example leaf thickness in the E. pauciflora $\times E$. Robertsoni combination, which by inspection seem to follow the same pattern.

A characteristic of segregating progeny derived from hybrids is that the variance of both morphological and oil characters is much greater than that of the parent species. If the facts disclosed so far have a more general application, they suggest that a recombinant between high yield and desirable oil constituents may be found if suitable segregating populations are produced.

The pattern of variation assessed by Willis *et al.* (1951) in the progeny from presumed forms of *E. maculata* shows close analogy with the segregating hybrid populations described above. It is suggested that the origin of these variants is by hybridization between *E. citriodora* and *E. maculata*. The most closely occurring *E. citriodora* trees, which in this case could be one parent, are believed to be about 40 miles distant from the above forms which occur in a *E. maculata* stand. Isolated hybrid individuals have been found at this and greater distances and may arise either from long-range outcrossing, for example by birds, or as the result of species population movements associated with climatic change. It is not difficult to imagine the origin of such individuals if they are hybrid, and it is suggested, therefore, that this is the explanation for them.

Conclusions.

It is clear that oil characters, both in yield and make-up, are strongly inherited in Eucalyptus, although the determination of the precise pattern will need a good deal more study. So long as evidence is still lacking that Eucalyptus oil is either an attractant or repellent to insects the function of oil in this regard can only be presumed. From the point of view of the Eucalyptus oil industry, three main lines for developing improved forms are clearly indicated. First and most obviously is the raising of plants from seed from selected stands with known desirable oil characters, as already initiated by Willis; secondly, raising segregating populations from selected naturally-occurring F1 hybrids with a view to obtaining superior recombinants; thirdly, producing experimentally F1 hybrids between parents which have separate desirable characters which, if combined together, would give individuals superior to either parent. It is of particular interest that in some combinations the oils display characters which transcend in magnitude those of either of the parents. This suggests that the biochemical processes resulting in oil formation may be, as in other plants, subject to separate genetic control at each of a number of steps, and that at times in hybrids some steps may be characteristic of one parent leading to the formation of a precursor which is then subject to genetically determined influences derived from the other parent somewhat in the manner suggested for the carotenoid pigment system of tomato (Tomes et al., 1952). Such a process could lead to the formation of compounds in greater quantity than those present in either parent species or even to compounds present in neither. Very much more study and experiment would be necessary to predict reasonably when and how this sort of change would occur. However, the likelihood that it is present offers very considerable possibilities in a breeding programme for improved oil production.

It suggests considerable flexibility in evolutionary aspects in the genus if oil is significant in this regard.

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